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LATITUDINAL VARIATION IN REPRODUCTIVE STRATEGIES BY THE MIGRATORY LOUISIANA WATERTHRUSH

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Abstract. We evaluated hypotheses that seek to explain breeding strategies of the Louisiana Waterthrush (*Parkesia motacilla*) that vary across a latitudinal gradient. On the basis of data from 418 nests of color-banded individuals in southwestern Pennsylvania and 700 km south in the Georgia Piedmont, we found that clutch size in replacement nests and probability of renesting were significantly greater in Pennsylvania (clutch size 4.4; renesting probability 0.66) than in Georgia (clutch size 3.8; renesting probability 0.54). Contrasts of the remaining measures of breeding were not statistically significant, and, in particular, mean daily nest survival in the two study areas was nearly identical (0.974 in Pennsylvania; 0.975 in Georgia). An individual-based model of fecundity (i.e., number of fledged young per adult female), predicted that approximately half of the females in both Pennsylvania and Georgia fledge at least one young, and mean values for fecundity in Pennsylvania and Georgia were 2.28 and 1.91, respectively. On the basis of greater support for the food-limitation hypothesis than for the season-length hypothesis, the trade-off between breeding in a region with more food but making a longer migration may be greater for waterthrushes breeding farther north than for those breeding farther south.

Key words: *fecundity, latitudinal variation, neotropical migrant, stochastic individual-based model, life history components, Louisiana Waterthrush,* Parkesia motacilla.

Variación Latitudinal en Estrategias Reproductivas de la Especie Migratoria *Parkesia motacilla*

Resumen. Evaluamos hipótesis que buscan explicar las estrategias reproductivas de *Parkesia motacilla*, que varían en un gradiente latitudinal. Con base en datos de 428 nidos de individuos marcados con anillos de colores en el sudoeste de Pensilvania y 700 km al sur en el piedemonte de Georgia, encontramos que el tamaño de la nidada en nidos de reemplazo y la probabilidad de anidación repetida fueron significativamente mayores en Pensilvania (tamaño de nidada 4.4; probabilidad de anidación repetida 0.66) que en Georgia (tamaño de nidada 3.8; probabilidad de anidación repetida 0.54). Las comparaciones de las demás medidas relacionadas con la reproducción no fueron estadísticamente significativas y, en particular, la supervivencia diaria de los nidos fue casi idéntica en las dos áreas de estudio (0.974 en Pensilvania; 0.975 in Georgia). Un modelo de la fecundidad basado en individuos (i.e., el número de volantones emplumados por hembra adulta) predijo que aproximadamente la mitad de las hembras tanto en Pensilvania como en Georgia produjeron al menos un volantón y los valores medios de fecundidad fueron de 2.28 y 1.91 en Pensilvania y Georgia, respectivamente. Sobre la base de un mayor respaldo a la hipótesis de limitación de alimento que a la de extensión de la temporada, el compromiso de reproducirse en una región con más alimento pero realizar una migración más extensa podría ser mayor para los individuos que se reproducen más al norte que para los que lo hacen más al sur.

INTRODUCTION

Birds that migrate long distances must allocate their reproductive effort to allow sufficient time and energy to survive journeys to their wintering grounds (Stearns 1976, Drent and Daan 1980, Alerstam et al. 2003). For these species, the breeding season is shorter and birds are less likely to make multiple nesting attempts than for the permanent residents that occur with them (Böhning-Gaese et al. 2000, Bruderer and Salewski 2009). However, because many long-distance migrants breed across a broad latitudinal gradient, they may well adopt strategies that are suited to local environmental conditions (Alerstam 1990). Understanding geographic variation in breeding strategies is important not only in understanding life histories (McNamara et al. 2008) but also for evaluating responses of species, communities, and ecosystems to changing climatic

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and land-use patterns (Coppack and Pulido 2004, Pulido and Berthold 2004, Knowlton and Graham 2010).

Provided that there is a latitudinal gradient in breeding strategy, at least two non-mutually exclusive hypotheses can be used to explain observed patterns of latitudinal gradients in reproductive strategies by long-distance (i.e., intercontinental) migrants breeding in the Northern Hemisphere (Table 1). First, long-distance migrants may increase their opportunities for renesting (i.e., following nest failure) by breeding toward the southern extent of their range. Here, the temperature extremes are moderated, the nesting season is longer, and these migrants need expend less energy daily and therefore have a slower metabolic rate while breeding (Weathers 1979). Under this season-length hypothesis, in comparison to birds nesting farther north, migrants nesting farther south should experience a longer breeding season (with less metabolic stress) and, therefore, have greater opportunities for multiple nesting attempts with potentially more days between attempts.

A second hypothesis posits that food availability during the breeding season may be greater in more northern areas than farther south because of increased day length (Thiollay 1988, Huston and Wolverton 2009), and that food availability constrains reproduction. Under this food-limitation hypothesis, clutch size (Lack 1947, 1948, Ashmole 1963) and, by extension, probability of renesting should be higher at northern latitudes than at southern latitudes. Also, under the food-limitation hypothesis, nest survival should increase with latitude. Females tend to make less frequent trips to and from the nest in areas with greater food availability (Chalfoun and Martin 2007), and this may be correlated with nest survival (Zanette et al. 2006). With the exception of probabilities of renesting and double brooding, the patterns predicted by the season-length and food-limitation hypotheses are identical (Table 1). Probabilities of renesting and double brooding, therefore, may be particularly useful for distinguishing which of the two hypotheses is a better descriptor of variation in breeding biology along a latitudinal gradient.

The Louisiana Waterthrush (*Parkesia motacilla*) is a songbird that migrates between the Nearctic and Neotropical regions and breeds from the coastal plain of the southeastern U.S. to the northern end of the Appalachian Mountains in the northeastern U.S. It nests along headwater streams in forests with an open understory and forages in and along streams for a wide variety of terrestrial and aquatic macroinvertebrates; it winters in similar habitat in the Greater Antilles and Middle America (Mattsson et al. 2009). Its ground-nesting, migratory, and vocal behaviors, combined with the broad latitudinal spread of its breeding distribution, make it a useful model species for examining variation in the breeding biology of a long-distance migrant along a latitudinal gradient.

TABLE 1. Expected trends with increasing latitude in measures of Louisiana Waterthrush breeding, based on two hypotheses for drivers of fecundity (i.e., number of young fledged per adult female). Descriptions of variables reflect their use for comparison of breeding strategies in southwestern Pennsylvania (Mulvihill et al. 2008, 2009, this paper) and in the Georgia Piedmont (Mattsson and Cooper 2007).

	Expected trend with increasing latitude[a]		
Field measurement	Season length	Food limitation	Description or individual-based calculation
Daily nest survival	—	↑	Daily nest-survival rate (Hazler 2004)
Nestling survival[b]	—	↑	No. young fledged/no. eggs laid
Egg-laying rate—1st nest[c,d]	—	↑	No. eggs laid in 1st nest/maximum clutch size in region
Egg-laying rate—replacement nest[b,c,d]	—	↑	No. eggs laid in replacement nest/maximum clutch size in region
Probability of renesting[e,f]	↓	↑	Probability that female renests after nest failure
Probability of 2nd brood[e,f]	↓	↑	Probability that female lays eggs while juvenile from 1st brood lives
Interval of renesting[b,c]	↓	↓	No. days between failure of previous attempt and egg laid in replacement nest
Interval of 2nd brood[b,c]	↓	↓	No. days between fledging of 1st brood and laying of 2nd clutch
Nest-cycle length[c,f]	—	—	No. days from completion of egg laying to fledging
Breeding-season length[g]	↓	—	No. days between date of egg laying for 1st nests and final nests

[a] Up arrow (↑) indicates that value is expected to increase in magnitude with increasing latitude; down arrow (↓) indicates that value is expected to decrease with decreasing latitude; dash (—) indicates no expected relationship between variable and latitude.
[b] Monitored previous nest by banded female.
[c] Date of hatching or laying known.
[d] Mean clutch size can be derived by multiplying rate of egg laying by maximum clutch size in region.
[e] Certain at least one young ready to fledge.
[f] Territory revisited at least weekly for 4 weeks after nest failed or fledged.
[g] Dates of both hatching and laying known; females without replacement nests or second broods excluded.

We compared the waterthrush's life-history strategies during the breeding season across a wide latitudinal gradient on the basis of two multi-year studies. In particular, we documented the fates of multiple nesting attempts by individual waterthrushes over 4 years in the Piedmont of north-central Georgia (Mattsson and Cooper 2007) and over 14 years in the Allegheny Mountains of southwestern Pennsylvania (Mulvihill et al. 2009); these study sites are separated by ~6° of latitude (700 km). Here, we describe reproductive strategies at each site by using estimates of quantities associated with breeding as well as an individual-based model of fecundity that used these estimates as inputs. We examined these results to assess hypotheses that explain latitudinal gradients in reproductive strategies, placing our findings within a more general context for understanding latitudinal shifts in patterns of breeding of long-distance migrants. To our knowledge, this is the first comprehensive effort to compare measures of reproduction (e.g., clutch size, renesting, and nest survival) of a long-distance migrant across a latitudinal gradient.

METHODS

STUDY SITES AND DATA COLLECTION

We analyzed two independent data sets on waterthrush reproduction, one from the Georgia Piedmont (33° 32′ N, 83° 32′ W; Mattsson and Cooper 2007) and one from southwestern Pennsylvania (40° 2′ N, 79° 17′ W; Mulvihill et al. 2009). The length of the growing season in the Georgia Piedmont exceeds that in southwestern Pennsylvania by ~60 days (National Climatic Data Center 2008). Linear waterthrush territories in Georgia (520 ± 40 m [mean ± 95% CI]; Mattsson and Cooper 2009) are longer than those along circumneutral streams in Pennsylvania (370 ± 10 m; Mulvihill et al. 2008), which suggests that food availability is greater in Pennsylvania than in Georgia, in accordance with the food-value theory (Stenger 1958). These studies used similar sampling methods, allowing direct comparisons of the results.

In Georgia, our study took place in 13 forested headwater drainages of the Southern Piedmont as part of a larger study examining the usefulness of the waterthrush as a bioindicator and multi-scale extrinsic drivers of its reproduction (Mattsson and Cooper 2006, 2009). Nine of the drainages are in the Upper Oconee River basin near Watkinsville, and four are in the Upper Ocmulgee River basin in Piedmont National Wildlife Refuge. From 2002 to 2005 we monitored nests along 2- to 3-km reaches within ten rural drainages and in 2004 added three forested riparian segments that were surrounded by urban land use.

In the mountains of western Pennsylvania, we monitored breeding waterthrushes intensively as part of broader studies of the ecological health of forested headwater streams throughout the state (O'Connell et al. 2003, Mulvihill et al. 2008). Study sites included 2- to 3-km reaches of circumneutral streams (pH ~7; *n* = 8), as well as others negatively affected by acid drainage from mines and/or acidic precipitation (pH range 4.5–5.5; *n* = 5). We monitored waterthrush reproduction along each of the 13 streams for 2 to 14 years (mean = 5.2, median = 3) from 1996 to 2009.

Beginning in late March or early April, we located waterthrush nests by systematically searching bank crevices and by following color-banded adults as they constructed their nests or fed young. Once nests were located, observers monitored them every 2–4 days, recording number of eggs or nestlings and documenting evidence of nest failure or fledging. We were successful at documenting nearly all nesting attempts of every pair of waterthrushes in our study areas. Nests were most often found during the building, laying, or incubation stages. If we did not observe clutch initiation directly, we estimated its date by backdating from observed dates of hatching or fledging, assuming a 13-day incubation period (beginning with the last egg laid) and a 10-day nestling period (Mattsson et al. 2009). If we did not observe hatching directly, we estimated the ages of nestlings from dates of laying, by backdating from dates of fledging, or on the basis of developmental (e.g., feathering) stage (Eaton 1958). We used observations of banded fledglings and/or of adults carrying food to confirm nesting success, considering nests successful if at least one young fledged. More details on data collection and preparation for analysis were reported by Mattsson and Cooper (2007) and Mulvihill et al. (2008).

STATISTICAL ANALYSES

To evaluate the "season-length" and "food-limitation" hypotheses for describing differences in the patterns of drivers for waterthrush reproduction between our two study areas, we compared estimates of various factors (Tables 1 and 2) and fecundity (i.e., number of fledged young per adult female) based on field data. The factors include the number of eggs laid, number of young fledged, nest-survival rate, length of time between nesting attempts, and probabilities of renesting and double brooding. With these estimates, we used a stochastic individual-based model to compare the fecundity of the waterthrush in the two study areas (Mattsson and Cooper 2007). Because of the alternative method we used for estimating the length of the breeding season (Table 1), results in this paper for Georgia differ somewhat from those presented in Mattsson and Cooper (2007). We calculated proportional differences between estimates as (higher – lower)/lower and inferred that differences were statistically significant if the 95% confidence interval for one area did not overlap the mean for the other area.

RESULTS

On the basis of our analysis of data from 418 nests at either end of a 700-km latitudinal gradient, values of three of 12 factors were significantly greater in southwestern Pennsylvania (PA) than they were in the Georgia Piedmont (GA; Table 2). Significant differences in means between the areas included probability of renesting (PA > GA by 21.4%), clutch size in replacement nests (PA > GA by 15.1%), and egg-laying rate (i.e.,

TABLE 2. Field-based estimates of measures of breeding in analysis of individual-based models of Louisiana Waterthrush fecundity in southwestern Pennsylvania (Mulvihill et al. 2008, 2009, this paper) and in the Georgia Piedmont (Mattsson and Cooper 2007). Values in bold differ significantly by region.

	Southwestern Pennsylvania					Georgia Piedmont				
Variable	Nests	Mean	Var.[a]	95% CL[a]	5–95th percentiles[b]	Nests	Mean	Var.[a]	95% CL[a]	5–95th percentiles[b]
Daily nest survival[c]	228	0.974	0.000	0.97–0.98	0.50–1.00	190	0.975	0.000	0.97–0.98	0.67–1
Nestling survival[c]	146	0.911	0.000	0.88–0.92	0.60–1.00	123	0.902	0.000	0.87–0.92	0.50–1
Egg-laying rate—1st nest[c,d]	194	0.806	0.026	0.78–0.83	0.00–1.00	105	0.790	0.028	0.76–0.82	0.67–0.83
Egg-laying rate—replacement nest[c,d]	**55**	**0.730**	**0.033**	**0.68–0.78**	**0.50–0.83**	**26**	**0.635**	**0.039**	**0.56–0.71**	**0.50–0.83**
Clutch size—1st nest	194	4.836	0.156	4.68–4.98	0.00–6.00	105	4.743	0.166	4.54–4.92	4.00–5
Clutch size—replacement nest	**55**	**4.382**	**0.197**	**4.08–4.65**	**3.00–5.00**	**26**	**3.808**	**0.232**	**3.34–4.24**	**3.00–5**
Probability of renesting[c]	**120**	**0.658**	**0.002**	**0.57–0.74**	**0.00–1.00**	**67**	**0.542**	**0.008**	**0.42–0.66**	**0.00–1**
Probability of 2nd brood[c]	143	0.056	0.000	0.03–0.11	0.00–1.00	83	0.084	0.001	0.04–0.17	0.00–1
Interval of renesting[e]	54	7.463	20.2	6.52–8.73	3.00–16.4	29	6.59	100	5.83–7.56	4.00–12
Interval of 2nd brood[e]	8	9.375	16.7	7.14–13.7	5.00–15.0	4	12.75	81.9	9.77–18.4	8.00–17
Nest-cycle length[f]	145	22.9	0.311	21.9–24.0	22.0–24.0	34	21.7	1.01	21.3–22.0	20.0–24
Breeding-season length[f]	228	41				190	49			

[a] Variance and confidence limits were calculated on the basis of variability among individual nest attempts.

[b] Percentiles represent extreme values recorded for individuals in the population.

[c] Beta-binomial sampling distribution used in fecundity simulation.

[d] Egg-laying rates based on a maximum clutch size of 6.

[e] Gamma sampling distribution used in fecundity simulation.

[f] Parameter was held fixed as the difference between 5th and 95th percentiles for dates of first eggs in each study area.

proportion of the maximum regional clutch size) in replacement nests (PA > GA by 15.0%). Nonsignificant differences in mean values between the areas included probability of a second brood (GA > PA by 50.0%), interval between the first and a second brood (GA > PA by 36.0%), and interval between failure of a nest and laying in the subsequent replacement nest (PA > GA by 13.2%). The mean values of the remaining factors differed by ≤ 6%. Mean daily nest survival in the two study areas was virtually identical.

Analyses based on a stochastic individual-based model (Fig. 1) predicted that approximately half of the females in Pennsylvania (48.5%) and in Georgia (48.5%) should fledge

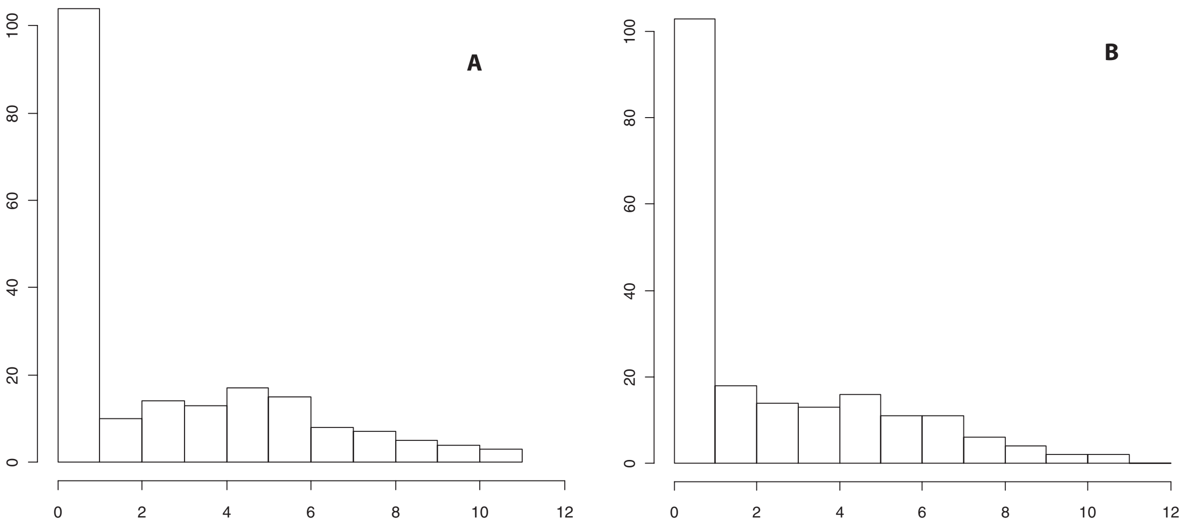

FIGURE 1. Histograms comparing the number of fledglings per adult female (i.e., fecundity) in southwestern Pennsylvania (A) to that in the Georgia Piedmont (B). Frequencies derived from an individual-based model ($n = 200$ females).

≥1 young. Maximum values of fecundity were 10 and 8 in Pennsylvania and Georgia, respectively. The mean values for fecundity in Pennsylvania and Georgia were 2.28 ± 2.82 SD and 1.91 ± 1.80 SD, respectively (19% difference in means), but broad overlap of these distributions precluded a statistically significant difference (Fig. 1).

DISCUSSION

Our comparison of the breeding biology of the Louisiana Waterthrush in two regions separated by ~6° of latitude or 700 km indicated that while fecundity and several other measures of breeding are very similar in the two regions, clutch size in replacement nests and probability of renesting were greater in Pennsylvania than in Georgia. On the basis of these differences, we can infer at least some latitudinal gradient in the species' breeding strategy. Similarities in the remaining factors may reflect either similarity of environmental conditions in the two regions or evolutionarily recalcitrant life-history traits. Both study areas are characterized by forested headwater streams, where the input of groundwater combined with shade provided by the canopy may moderate stream temperatures along this latitudinal gradient (Barton et al. 1985, Osborne and Kovacic 1993). It is difficult, therefore, on the basis of this analysis to discern among the possible mechanisms driving the similarities in breeding strategies in the two regions. Our findings were based on a comprehensive comparison of breeding biology in each region and, taken together, provide more support for the food-limitation hypothesis than for the season-length hypothesis in explaining the differences in the Louisiana Waterthrush's reproductive strategies along a latitudinal gradient. That clutch size in replacement nests and probability of renesting were higher in the northern study area than in the southern study area lends some robust support for the food-limitation hypothesis over the season-length hypothesis.

In our comprehensive examination, we found limited, if any, support for the season-length hypothesis, which posits that farther south, where low temperatures are moderated, migrants need to expend less energy, have lower metabolic demand, and, therefore have greater opportunity to attempt multiple nests. Though not statistically significant, the greater interval between broods in Georgia may lend some support to the season-length hypothesis. In comparison to those in the Georgia Piedmont, waterthrushes in southwestern Pennsylvania had a greater likelihood of renesting following nest failure, a similar likelihood of initiating a second brood following a successful nest, a similar interval between a failed first nest and a replacement nest, a breeding season of similar length, and a similar interval between a successful first nest and a second nest. Such limited support for the season-length hypothesis may be explained by a combination of traits that are plastic (e.g., interval between a successful first nest and a second nest) and those that are recalcitrant (e.g., probability of a second brood and length of breeding season) with respect to latitude-induced environmental variation (Coppack and Pulido 2004, Pulido and Berthold 2004). Experimental studies have found support for the season-length hypothesis in that individuals translocated across latitudinal gradients are plastic with respect to length of breeding season (for review see Coppack 2007).

We found more convincing, albeit limited, support for the food-limitation hypothesis, which asserts that greater availability of food during the breeding season at higher latitudes leads to increased clutch size, nest survival, and probabilities of renesting and double brooding. Observed differences between study areas with respect to clutch size and probability of renesting supported the food-limitation hypothesis; however, comparisons of nest survival, nestling survival, and probability of a second brood failed to support this hypothesis. When compared to waterthrushes in Georgia, those in Pennsylvania had an identical nest-survival rate, similar nestling-survival rate, similar clutch size in first nests, larger clutches in replacement nests, similar probability of a second brood, and a higher probability of renesting. As with the season-length hypothesis, these mixed results may be explained by recalcitrant traits and/or similarity of environmental conditions in the two study areas. Intraspecific and interspecific correlations between clutch size and latitude are rather pronounced in the Northern Hemisphere (Klomp 1970, Kulesza 1990), including passerines that migrate long distances (Dunn et al. 2000).

There are at least three additional considerations that could explain observed differences between Georgia and Pennsylvania in clutch size and probability of renesting. First, the gradient in clutch size was evident for replacement nests but not for first nests. This difference could be explained by the availability of food in the two study areas being similar during early spring but divergent later in the season following full leaf-out when waterthrushes shift toward a more terrestrial diet (Craig 1984). Second, several streams in Pennsylvania were acidic, and waterthrushes breeding along these streams have smaller clutches, reduced availability of aquatic prey, but similar nest survival than those breeding along circumneutral streams (Mulvihill et al. 2008). Our observation that clutches in replacement nests are larger in Pennsylvania than in Georgia, however, runs counter to the hypothesis that stream acidity drives patterns in clutch size along this latitudinal gradient. The effect of stream acidity on probability of renesting is uncertain because of the relatively high nest survival and low density of waterthrushes along acidic streams, but this is an area of future research.

Third, we studied the waterthrush's breeding biology in Pennsylvania for 2 to 14 years, that in Georgia for 3 years. The study period in Georgia and some streams in Pennsylvania, therefore, may misrepresent the species' breeding biology over the long term. In particular, annual variation in rainfall or other weather patterns may influence breeding biology. For example, in north-central Georgia, 2002 and 2004 were particularly dry years, 2003 was much wetter than average, with May 2003 having the second highest accumulated rainfall on record for that month (NWSFO 2004). It is possible that rainfall extremes may have depressed clutch sizes and renesting relative to a long-term average. Confirming this potential effect would support another rendition of the food-limitation hypothesis that explains variation in breeding biology across time rather than across latitudes. While extension of the hypothesis across time (years) remains to be examined, variation in weather may be expected to affect the waterthrush's breeding biology at different latitudes differently, especially in the face of a changing climate. With a warming climate, annual precipitation in both the Piedmont (Mulholland et al. 1997) and the Mid-Atlantic region (Neff et al. 2000) is predicted to vary more widely. If temporal shifts in precipitation become decoupled, a latitudinal gradient may result.

The Louisiana Waterthrush, and perhaps songbirds migrating long distances in general, may experience a trade-off between breeding farther north, where more food is available but a longer migration is required, in comparison to areas farther south within the North Temperate Zone. When compared to waterthrushes breeding at the southern extent of their range, northern breeders appear to have a greater probability of renesting and larger clutches in replacement nests. According to our analysis of individual-based models, the distribution of values of females' fecundity in the two study areas was quite similar. In the face of the effects of climate change, especially when it is exacerbated by intensification of anthropogenic land use, local populations of long-distance migrants may struggle, at least initially, to adapt to corresponding shifts in length of breeding season, predation risk, and food availability. These species' relatively high mobility and phenotypic plasticity of reproductive strategies across a broad latitudinal range (Coppack and Pulido 2004, Visser et al. 2009), however, may bode well for their long-term persistence. Still, conservation strategies that allow adaptation to occur, such as promoting connectivity among habitat patches along elevational and latitudinal gradients, remain prudent, to help offset the risk that some species' traits are recalcitrant and could present problems for their resiliency to changing environmental conditions.

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